Plant physiology: **The importance of sucrose transporters**

Elisabeth Truernit

Sucrose transport is essential for the distribution of carbohydrates in plants. Recent studies have shown that a specific transporter protein plays an essential role in loading sucrose into the phloem component of the plant vasculature.

Address: Department of Plant Science, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK.
E-mail: ebt21@cam.ac.uk

Current Biology 2001, 11:R169–R171

0960-9822/01/$ – see front matter

Plant cells produce carbohydrates by the fixation of carbon dioxide during photosynthesis. In higher plants, however, not all cells are photosynthetically active: the roots, reproductive structures, developing organs and storage tissue rely entirely on the import of carbohydrates synthesised elsewhere in the plant. Mature leaves are the predominant sites of photosynthesis in a higher plant: they produce a surplus of carbohydrates, which is exported to other parts of the plant. Carbohydrate exporting tissue is often referred to as 'source tissue' and the importing tissue as 'sink tissue'.

Sucrose is the major transported form of carbohydrates in plants. Transport of sucrose between source and sink is mediated by a specific part of the vasculature, the phloem. The key components of the phloem are the sieve elements, in which long-distance transport occurs, and the closely associated companion cells. Sieve elements and companion cells are extensively interconnected by a high number of intercellular connections, called plasmodesmata; together, they form the sieve element–companion cell complex. In leaves, sucrose gets loaded into the minor veins of the phloem. There are two principal pathways for the delivery of sucrose into the minor vein sieve element–companion cell complex: symplastic loading, in which sucrose passes the entire route from the leaf mesophyll cells to the sieve element–companion cell complex in the so-called 'symplast', moving from cell to cell via plasmodesmata; and apoplastic loading, where sucrose is released from the mesophyll cells and then actively taken up by sucrose transporters located in the sieve element–companion cell complex (Figure 1).

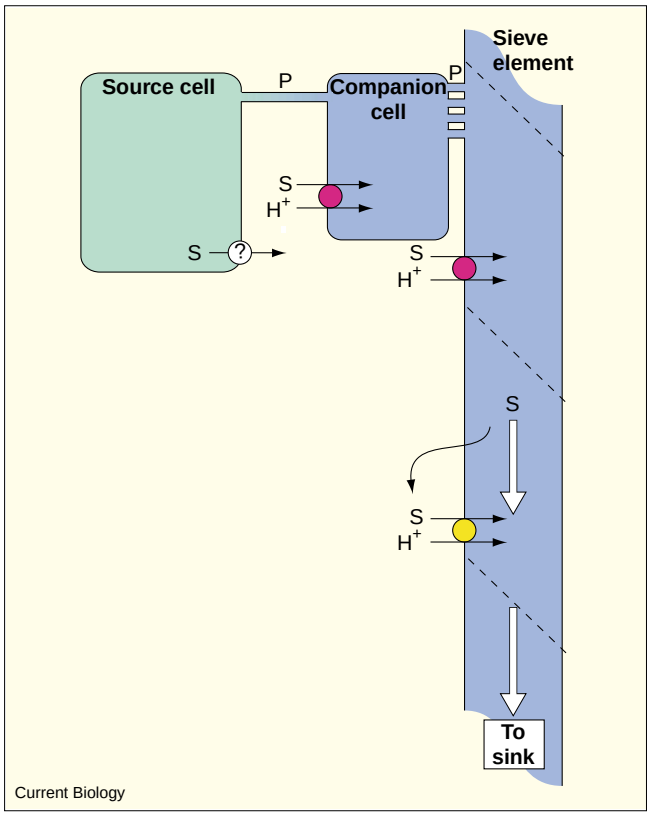
The extent to which plants can use either of the two pathways for sucrose delivery depends on the number of plasmodesmatal connections between the minor vein sieve element–companion cell complex and its surrounding cells, and this varies between species [1,2]. In many crop species, such as tobacco or potato, the sieve element–companion cell complex is almost symplastically isolated [1]. The sieve element–companion cell complex of *Arabidopsis* has more connections to its surrounding cells, but still the proposed route for sucrose loading involves the uptake of sucrose from the apoplast into the phloem by sucrose transporters [3]. Recently there have been considerable advances in understanding the role of sucrose transporters in plants, and one recent study in particular [4] has shown that a specific sucrose transporter plays an essential role in apoplastic phloem loading. But as more genes encoding plant sucrose transporters are identified, it is becoming evident that they are likely to have a variety of very distinct functions in plants.

An important step towards unveiling the function of sucrose transporters in higher plants was made when the first genes encoding plant sucrose transporters were cloned from spinach and potato [5,6]. *In situ* studies showed that the sucrose carrier from potato, StSUT1, is highly expressed in the phloem of the leaf minor veins, the major site of phloem loading [6]. StSUT1 is also expressed, though to lesser extent, in the stems and sink tissues, where the retrieval of sucrose leaking out of the phloem, and uptake of sucrose into the sink, respectively, have been proposed as possible functions of the transporter.

Further direct evidence for the importance of sucrose transporters in phloem loading came from studies of transgenic potato and tobacco plants. In these, antisense RNAs were used to reduce the level of the sucrose carrier SUT1 in the phloem [7–10]. The observed effects were in good agreement with the postulated function of SUT1 in phloem loading. The antisense plants had a retarded growth phenotype on soil, and their source leaves were found to export less carbohydrate. As a result of this, carbohydrates accumulated in the leaves and the sink organs were malnourished, resulting in a dramatically reduced tuber yield in the transgenic potato plants. These observations clearly show that sucrose transporters in the phloem are essential for carbohydrate partitioning, at least in tobacco and potato, both members of the Solanaceae family.

The kind of antisense inhibition used in these early experiments, however, could also have affected other members of the sucrose transporter family. To date, over twenty different genes for disaccharide transporters have been identified from various plant species, named either SUT or SUC, for sucrose transporter, or SCR for sucrose carrier [11,12]. So far, all of these transporters have been found to belong to the same gene family, the members of which encode highly hydrophobic dissaccharide transporters with twelve transmembrane-spanning helices. Many of

Figure 1



A model of the contribution of sucrose transporters to phloem loading. Sucrose (S) can pass the entire route from source cells to the sieve element–companion cell complex in the symplast moving from cell to cell via plasmodesmata (P). In many plant species, however, sucrose leaves the symplast at some point, possibly via sucrose efflux carriers (blue open circle). It then gets actively accumulated into the sieve element–companion cell complex by proton coupled sucrose carriers (pink circle) expressed in the companion cells and/or sieve elements. Sucrose carriers expressed in the phloem are also thought to retrieve sucrose that has been leaking out of the phloem on its way to sink tissues (yellow circle).

these transporters have been shown to mediate sucrose uptake and most likely function as proton-symporters, using a transmembrane proton gradient to drive sucrose transport. Recently, several papers [13–16] have reported the cloning of new members of this family from tomato, potato and *Arabidopsis*. It is more apparent now that a single plant species can have many different disaccharide transporter genes. These genes usually show significant sequence similarity and often overlap in their expression pattern. In tomato, for example, three members of the sucrose transporter family are expressed in sieve elements, and a distinct role in phloem loading has been suggested for each of them [13,16].

Gottwald *et al.* [4] took advantage of the genetic amenability of the model plant *Arabidopsis thaliana* in order to analyse sucrose transporter function. They screened for mutants where insertion of the T-DNA from *Agrobacterium tumefaciens* had inactivated a sucrose transporter gene, and identified three lines with a T-DNA insertion in different regions of the *AtSUC2* gene. The overall expression pattern and predicted function of the AtSUC2 transporter has been shown previously to be very similar to those reported for SUT1, although AtSUC2 is located in companion cells rather than sieve elements [17,18].

The three *AtSUC2* mutant lines [4] all showed a similar phenotype. They were indistinguishable from wild-type plants when grown on media containing sucrose. When grown without sucrose, however, the homozygous mutant plants were smaller than wild type, had yellowing translucent cotyledons and short primary roots, and did not develop beyond this stage unless rescued by transferring onto media containing 1% sucrose. When plants grown on sucrose were transferred to soil, they developed more slowly than wild type, showed stress symptoms such as accumulation of anthocyanins, and did not produce viable seed. The longer the plants remained on sucrose-containing media, the better they grew when transferred to soil. When source leaves were fed with radioactive sucrose, the accumulation in sink organs seen with the wild type was not observed with the mutant, indicating that sucrose cannot be exported from the mutant leaves.

In view of the earlier results from antisense inhibition [7–10], the new results obtained by Gottwald *et al.* [4] are not surprising. The phenotype of the *AtSUC2* mutants is very similar to that of the *SUT1* antisense plants. This strongly suggests that in *Arabidopsis*, as in the Solanaceous species, apoplastic loading mediated by a sucrose transporter is an essential step. Moreover, this is the first time that the availability of T-DNA knockout *Arabidopsis* plants has been exploited to study sucrose transporter function, opening exciting new prospects for the analysis of plant carbohydrate partitioning. The data show that it is now possible to investigate precisely the effects of the absence of one specific sucrose transporter in plants. It will now be possible to study the effects of inactivating several transporter genes in a single plant, or to screen for genes that can rescue the knockout phenotypes.

The recent completion of the *Arabidopsis* genome sequence has provided a global view of its transporter gene content. So far, seven different genes — including *AtSUC2* — have been identified that code for proteins similar in sequence to sucrose transporters. To date, the proteins encoded by five of those genes have been characterised: they all transport sucrose, but they differ in kinetic properties, substrate specificity and expression patterns. In addition to AtSUC2, AtSUT4 appears to be expressed in the phloem, but predominantly in minor veins [16]. Some are not expressed in the phloem at all, but in cells close to the phloem in the case of AtSUC3

(also named AtSUT2) [13,15], or in floral tissue in the case of AtSUC1 [19]. Disaccharide transporters are thus likely to have a number of distinct functions in plants. In some sink cells, for example, they may be involved in carbohydrate uptake from the apoplast, as has been suggested for hexose transporters expressed in the sink [11]. They are also thought to play a role in sugar sensing [13,15], and may be essential for the uptake of other substances — for example, there is evidence that AtSUC5 is involved in vitamin uptake [14]. It will be fascinating to discover the variety and complexity of different tasks these proteins have within a plant.

Acknowledgements

I am grateful to Mark Tester and Smita Kurup for critical reading of the manuscript.

References

1. Gamalei Y: Phloem loading and its development related to plant evolution from trees to herbs. *Trees* 1991, 5:50-64.
2. Van Bel AJE, Gamalei YV, Ammerlaan A, Bik LPM: Dissimilar phloem loading in leaves with symplasmic or apoplasmic minor-vein configurations. *Planta* 1992, 186:518-525.
3. Haritatos E, Medville R, Turgeon R: Minor vein structure and sugar transport in ***Arabidopsis thaliana***. *Planta* 2000, 211:105-111.
4. Gottwald JR, Krysan PJ, Young JC, Evert RF, Sussman MR: Genetic evidence for the ***in planta*** role of phloem-specific plasma membrane sucrose transporters***.*** *Proc Natl Acad Sci USA* 2000, 97:13979-13984.
5. Riesmeier JW, Willmitzer L, Frommer WB: Isolation and characterization of a sucrose carrier cDNA from spinach by functional expression in yeast. *EMBO J* 1992, 11:4705-4713.
6. Riesmeier JW, Hirner B, Frommer WB: Potato sucrose transporter expression in minor veins indicates a role in phloem loading. *Plant Cell* 1993, 5:1591-1598.
7. Riesmeier JW, Willmitzer L, Frommer WB: Evidence for an essential role of the sucrose transporter in phloem loading and assimilate partitioning. *EMBO J* 1994, 13:1-7.
8. Kühn C, Quick WP, Schulz A, Riesmeier JW, Sonnewald U, Frommer WB: Companion cell-specific inhibition of the potato sucrose transporter SUT1. *Plant Cell Environ* 1996, 19:1115-1123.
9. Lemoine R, Kühn C, Thiele N, Delrot S, Frommer WB: Antisense inhibition of the sucrose transporter in potato: effects on amount and activity. *Plant Cell Environ* 1996, 19:1124-1131.
10. Bürkle L, Hibberd JM, Quick WP, Kühn C, Hirner B, Frommer WB: The H^+-sucrose cotransporter NtSUT1 is essential for sugar export from tobacco leaves. *Plant Physiol* 1998, 118:59-68.
11. Williams LE, Lemoine R, Sauer N: Sugar transporters in higher plants — a diversity of roles and complex regulation. *Trends Plant Sci* 2000, 5:283-290.
12. Lemoine R: Sucrose transporters in plants: update on function and structure. *Biochim Biophys Acta* 2000, 1465:246-262.
13. Barker L, Kühn C, Weise A, Schulz A, Gebhardt C, Hirner B, Hellmann H, Schulze W, Ward JM, Frommer WB: SUT2, a putative sucrose sensor in sieve elements. *Plant Cell* 2000, 12:1153-1164.
14. Ludwig A, Stolz J, Sauer N: Plant sucrose-H^+ symporters mediate the transport of vitamin H. *Plant J* 2000, 24:503-509.
15. Meyer S, Melzer M, Truernit E, Hümmer C, Besenbeck R, Stadler R, Sauer N: AtSUC3, a gene encoding a new ***Arabidopsis*** sucrose transporter, is expressed in cells adjacent to the vascular tissue and in a carpel cell layer. *Plant J* 2000, 24:869-882.
16. Weise A, Barker L, Kühn C, Lalonde S, Buschmann H, Frommer WB, Ward JM: A new subfamily of sucrose transporters, SUT4, with low affinity/high capacity localized in enucleate sieve elements of plants. *Plant Cell* 2000, 12:1345-1355.
17. Truernit E, Sauer N: The promoter of the ***Arabidopsis thaliana*** SUC2 sucrose-H^+ symporter gene directs expression of β-glucuronidase to the phloem: evidence for phloem loading and unloading by SUC2. *Planta* 1995, 196:564-570.
18. Stadler R, Sauer N: The ***Arabidopsis thaliana*** AtSUC2 gene is specifically expressed in companion cells. *Bot Acta* 1996, 109:299-306.
19. Stadler R, Truernit E, Gahrtz M, Sauer N: The AtSUC1 sucrose carrier may represent the osmotic driving force for anther dehiscence and pollen tube growth in ***Arabidopsis***. *Plant J* 1999, 19:269-278.